

# Climate change and the effects of temperature extremes on Australian flying-foxes

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Little is known about the effects of temperature extremes on natural systems. This is of increasing concern now that climate models predict dramatic increases in the intensity, duration and frequency of such extremes. Here we examine the effects of temperature extremes on behaviour and demography of vulnerable wild flying-foxes (*Pteropus* spp.). On 12 January 2002 in New South Wales, Australia, temperatures exceeding 42°C killed over 3500 individuals in nine mixed-species colonies. In one colony, we recorded a predictable sequence of thermoregulatory behaviours (wing-fanning, shade-seeking, panting and saliva-spreading, respectively) and witnessed how 5–6% of bats died from hyperthermia. Mortality was greater among the tropical black flying-fox, *Pteropus alecto* (10–13%) than the temperate grey-headed flying-fox, *Pteropus poliocephalus* (less than 1%), and young and adult females were more affected than adult males (young, 23–49%; females, 10–15%; males, less than 3%). Since 1994, over 30 000 flying-foxes (including at least 24 500 *P. poliocephalus*) were killed during 19 similar events. Although *P. alecto* was relatively less affected, it is currently expanding its range into the more variable temperature envelope of *P. poliocephalus*, which increases the likelihood of die-offs occurring in this species. Temperature extremes are important additional threats to Australian flying-foxes and the ecosystem services they provide, and we recommend close monitoring of colonies where temperatures exceeding 42.0°C are predicted. The effects of temperature extremes on flying-foxes highlight the complex implications of climate change for behaviour, demography and species survival.

**Keywords:** global change; heat waves; fruit bats; Chiroptera

## 1. INTRODUCTION

Over the past 100 years, the global average temperature has increased by approximately  $0.74 \pm 0.18^\circ\text{C}$  (Mean  $\pm$  s.e.) and is projected to continue to rise at a rapid rate (IPCC 2007). Changes in climate are significant for natural systems as they can affect population abundance, shifts in species range distributions and the number of species invasions and extinctions (Humphries *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Thomas *et al.* 2004). Recently, extreme weather events have gained in importance relative to gradual climatic trends as mechanistic drivers of broad ecological responses to climatic change (Parmesan *et al.* 2000). Temperature extremes that exceed physiological limits can cause widespread mortality, as evidenced by the 2003 heat wave in Europe that resulted in more than 15 000 human fatalities in France alone (WHO 2003). However, very little is known about the kinds of effects that temperature extremes have on natural systems. This is a matter of increasing concern now that current climate models predict a dramatic increase in the frequency, intensity and duration of temperature extremes (Meehl & Tebaldi 2004), through the combined effects of a shift towards warmer

(Easterling *et al.* 2000a) and more variable temperatures (Schär *et al.* 2004).

In this study, we examined the effects of temperature extremes on the behaviour and demography of Australian flying-foxes (*Pteropus* spp.). The grey-headed flying-fox (*Pteropus poliocephalus*) and the black flying-fox (*Pteropus alecto*) are among the largest species of fruit bats (Hall & Richards 2000). *Pteropus poliocephalus* is endemic to coastal southeastern Australia and it extends into higher latitudes than any other pteropodid (Mickleburgh *et al.* 1992). In northern New South Wales (NSW) and southern Queensland (QLD), *P. poliocephalus* shares colonies with *P. alecto* (Hall & Richards 2000). The range of *P. alecto* extends from Papua New Guinea and Indonesia into the forested areas of northern NSW along the east coast of Australia. At night, both pteropodids forage for nectar, pollen and fruit, and during the day they roost in large aggregations (colonies/roosts/camps) that may contain thousands of individuals (e.g. Tidemann 1999; Markus & Hall 2004). They provide important ecosystem services, including pollination of wild and cultivated crops and seed dispersal (e.g. Fujita & Tuttle 1991). However, they are exposed to threatening anthropogenic factors (Mickleburgh *et al.* 1992), the most serious of which are ongoing loss of foraging and roosting habitat (e.g. Tidemann 1999), direct killing of animals in orchards and harassment and destruction of roosts

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(e.g. Tiedemann & Vardon 1997). The species are listed as Vulnerable on the NSW Threatened Species Conservation Act 1995 (*P. alecto* and *P. poliocephalus*), and the Commonwealth Environment Protection and Biodiversity Conservation Act 1999 (*P. poliocephalus*). Because flying-foxes roost among the exposed branches of canopy trees, they are particularly sensitive to the effects of extreme temperatures, and therefore are convenient indicators for assessing the impact of temperature extremes on the natural environment.

On 12 January 2002, weather stations in coastal eastern Australia recorded maximum temperatures that were up to 16.5°C higher than the 30-year average mean daily maximum. This single extreme temperature event was associated with the death of thousands of flying-foxes, providing a unique opportunity to assess directly the effects of a temperature extreme on large terrestrial vertebrates. We recorded the effects of the temperature extreme on a mixed-species colony as the event was unfolding, and we present data on thermoregulatory behaviour and selective mortality. In addition, we related temperature and mortality across colony sites that were occupied at the time of the extreme. Finally, we present mortality and associated temperature data from 18 similar past extreme events.

## 2. MATERIAL AND METHODS

Our main study site (Dallis Park; 28°21'24" S, 153°23'06" E) is occupied by a mixed-species colony and is located near the southern end of the zone of range overlap between *P. poliocephalus* and *P. alecto*. The colony has been the subject of an intensive ecological study since 2000 (Welbergen 2005). On 12 January 2002, we documented individual behaviour, thermoregulatory responses and changes in roosting patterns, commencing at 06.00 hours until approximately 15.00 hours. At approximately 11.30 hours, the behaviour of animals started to depart notably from normal. Observations were supplemented by time-coded photographs.

On January 13 and 14, we systematically searched the Dallis Park colony and adjacent areas for corpses, and classified a total of 1361 bodies by species (i.e. *P. alecto* versus *P. poliocephalus*; Hall & Richards 2000). A subset of these ( $n=340$ ), confined to five randomly selected areas in the colony, was also classified by age and sex class (i.e. adult, young, female, male). Young were distinguished by their smaller body size and the sexes by external inspection of the genitalia. There was no difference between the species compositions of the full set and subset of corpses, and neither did the subset differ in terms of species, sex and age composition among the five randomly selected areas ( $\chi^2$  values on original data,  $p>0.05$ ).

Following the temperature extreme, 92 orphaned young with clear signs of dehydration were rescued by wildlife carers (Pinson 2007). Since young were found at random locations in the colony, we add their total to the total number of individuals that died, and allocate a proportional share (i.e.  $340/1361 \times 92 = 23$ ) to the subset of corpses that was classified by age and sex class.

During April 2001, January/February 2002 and April 2002, we also conducted detailed colony composition assessments. During these three periods, the colony was very constant in shape and size ( $1.3 \pm 0.1$  ha; Welbergen 2005). A fly out count (Eby 2000) and two extensive ground

counts (Welbergen 2005) resulted in population estimates of 30 800, 26 500 and 28 200, respectively. Relative proportions of species, age and adult sex classes were determined at 19, 19 and 29 sets of evenly spread GPS coordinates in the colony, respectively. At the coordinates we selected virtual columns from the ground up to the top of the vegetation. The diameter of the column was increased until it encompassed approximately 100 bats, which were then counted by species and age class (totals counted during the assessment periods: 1585, 2083 and 3069, respectively), and observed until more than one-third of the adults had been sexed (totals sexed: 578, 941 and 1536, respectively).

We use data from the National Flying-Fox Count (see Eby 2000), involving the locations of colonies that were known to be occupied during the 12 January 2002 temperature extreme. Colonies that had been affected by the temperature extreme were surveyed by J. Maisey. The number of deaths was estimated to the nearest 100, and species and age class as a percentage. Colony populations were estimated by ground counts from her experience of the sites. The Coffs Creek camp was surveyed by J. Wood and others.

Data on past flying-fox die-offs come from an exhaustive search of the literature, and consultations with the National Parks and Wildlife Service, as well as the Flying-Fox Information and Conservation Network (FFICN).

We use data from the Australian Bureau of Meteorology (ABM) including all 12 January 2002 temperature data from 332 QLD and NSW weather stations, as well as the absolute monthly maximum temperatures from all QLD and NSW weather stations that were operational at any time since 1800. Using ArcInfo, we selected all non-montane extremes from stations between 1 and 100 km from the coast to coincide with known distributions of colonies of *P. alecto* and *P. poliocephalus*.

Statistical tests were carried out in MINITAB for Windows (v. 14.0, Minitab, Inc.). All tests were two-tailed and significance was set at  $\alpha=0.05$ .

## 3. RESULTS AND DISCUSSION

As the temperatures were rising in the Dallis Park colony on 12 January 2002, both *P. alecto* and *P. poliocephalus* showed the following sequence of behaviours (see also figure 1 in the electronic supplementary material): (i) wing-fanning (start: approx. 10.00 hours), (ii) shade-seeking (start: approx. 11.15 hours), (iii) panting (start: approx. 13.15 hours) and (iv) saliva-spreading (start: approx. 13.45 hours). Later, individuals began falling from the trees (start: approx. 13.53 hours). Fallen individuals became increasingly lethargic and died within 10–20 min.

The behavioural sequence displayed by both species closely resembled that reported elsewhere and seems adaptive for maintaining body temperature ( $T_b$ ) against increasing ambient temperature ( $T_a$ ). Wing-fanning facilitates thermoregulation by forced convection (Laburn & Mitchell 1975) and shade-seeking lowers  $T_b$  by reducing direct radiation absorption from sunlight (Licht & Leitner 1967a). When the  $T_a$  exceeds  $T_b$ , wing-fanning and shade-seeking are no longer adequate for heat dispersal, but panting and saliva-spreading can still reduce  $T_b$  by increasing evapotranspiration (Licht & Leitner 1967b). The loss of body water will be significant, however, and animals should deploy only this strategy when  $T_b$  has risen close to lethal limits (Licht & Leitner 1967b).

Table 1. Demographic impact on the Dallis Park colony of 12 January 2002 temperature extreme in the Northern Rivers area. (Mortality figures in *italics* are significantly higher than their relevant comparisons (see text;  $\chi^2$ s on original data:  $>38.2$ ;  $p<0.001$  in all cases).)

	present <sup>a</sup> (min–max)	died <sup>b</sup>	percentage that died (min–max)
total	26 500–30 800	1453	5–6
<i>composition by species, age and sex class (%)</i>			
<i>P. alecto</i>	39–45	92	10–13
adults	35–37	54	7–9
females	17–22	47	10–15
males	15–18	7	2–3
juveniles	4–8	38	23–49
<i>P. poliocephalus</i>	55–61	8	<1
adults	46–50	1	<1
females	23–27	1	<1
males	22–25	0	0–0
juveniles	8–15	7	2–5

<sup>a</sup> Minimum and maximum estimates as determined by colony composition assessments conducted in 2001 and 2002.

<sup>b</sup> Total number and composition (in percentage species, age, and sex class) of individuals that died.

Animals started dying approximately 1 hour before the temperature at the nearest weather station reached an all time high of 42.9°C, which was 3.1 s.d. higher than the average monthly summer maximum (35.3°C), and a 13.8°C departure from normal. The same weather station recorded 40.2, 40.7, 40.9 and 41.2°C in summer 2002, 2001, 2004 and 1994, respectively, without any evidence of mortality.

The minimum number of bats that died in the colony on 12 January 2002 was 1453 (approx. 5–6% of the bats present; [table 1](#)). Mortality was significantly higher among *P. alecto* than *P. poliocephalus* (10–13% versus less than 1%,  $\chi^2$  values on original data  $>263.0$ ,  $p<0.001$ , [table 1](#)). This suggests that *P. alecto* has lower species-specific physiological limits for coping with high temperatures than *P. poliocephalus*.

Mortality was significantly higher among dependent *P. alecto* young than adults (23–49% versus 7–9%,  $\chi^2$  values on original data  $>65.4$ ,  $p<0.001$ , [table 1](#)). Given that young are generally less able to thermoregulate than adults (e.g. [Bartholomew et al. 1964](#)), we would expect young to be more affected by the temperature extreme. However, it is possible that some dependent young died not from acute hyperthermia but rather from starvation after becoming orphaned.

In addition, mortality was significantly higher among *P. alecto* females than males (10–15% versus 2–3%;  $\chi^2$  values on original data  $>38.3$ ,  $p<0.001$ , [table 1](#)). Since lactation may result in elevation of basal metabolic rate and increased thermoregulatory needs ([Brody 1974](#)), we would expect lactating females to have more difficulty keeping their  $T_b$  under lethal limits than males. We did not assess lactation in the Dallis Park colony, but a sample ( $n=33$ ) of females that died on 12 January 2002 in the Currie Park colony showed that 100% were lactating (J. Maisey 2002, unpublished data).

The temperature extreme of 12 January 2002 caused die-offs in at least nine colonies. All affected colonies

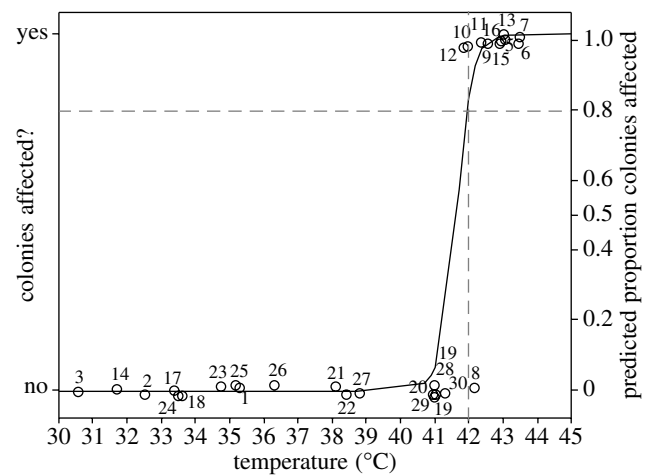


Figure 1. The colonies that were and were not affected versus the temperature recorded at their respective nearest weather station during the temperature extreme of 12 January 2002 in the Northern Rivers area, New South Wales, Australia (binary logistic regression:  $Z = -2.31$ ,  $p<0.021$ ; log likelihood =  $-5.766$ ;  $G = 26.659$ , d.f. = 1,  $p<0.001$ ; goodness of fit: Pearson's  $p>0.311$ ;  $x_{80\%} = 42.0^\circ\text{C}$ ). Colonies: 1, Singleton; 2, Wingham Brush; 3, Brombin; 4, Kooloonbung Ck; 5, Bellingen Island; 6, Coffs Creek; 7, Casino; 8, East Ballina; 9, Mollies Grass; 10, Lumley Park; 11, Currie Park; 12, Booyong; 13, Kyogle; 14, Ocean Shores; 15, Moore Park; 16, Dallis Park; 17, Cudgen; 18, Caddy's Island; 19, Woodburn; 20, Helensvale; 21, Slacks Creek Park; 22, Cleveland Park; 23, Griffin Park; 24, Hemmant Park; 25, Everton Park; 26, Sandgate; 27, Eudlo Creek; 28, Goat Island; 29, Cooloola; 30, North Creek.

experienced temperatures between 41.7 and 43.4°C; colonies experiencing temperatures below this range were not affected. There was a significant effect of the maximum temperature on the probability that a colony was affected, with 80% of colonies affected by temperatures exceeding 42.0°C ([figure 1](#)). All affected colonies were located in the Northern Rivers area along approximately 250 km of east Australian coastline, covering an area of approximately 11 000 km<sup>2</sup>. The collated number of individuals that died was 3679 ([table 2](#)), which is likely to be an underestimate because mortality data for some colonies were incomplete. In the subset of affected colonies for which demographic data were available, mortality was biased towards *P. alecto* ([table 2](#); Wilcoxon signed-rank test:  $n=6$ ,  $W=21$ ,  $p=0.032$ ), and the proportion of *P. alecto* that died increased with increasing temperature ([table 2](#); Pearson's correlation: 0.991;  $p<0.001$ ;  $n=5$ ).

An exhaustive literature search yielded evidence for at least 18 other die-off events since 1994 ([table 3](#); [figure 2](#)). Together they involved the death of more than 30 000 individuals. Some of the events arguably feature among the most dramatic die-offs ever recorded in nature. The estimated total that died is necessarily conservative since many colonies are in remote locations and not monitored regularly. The minimum and maximum number of individuals that were reported to have died during an event increased significantly with the maximum recorded temperature ([table 3](#); Pearson's correlations: 0.543;  $p=0.037$ ;  $n=15$ ; and 0.563;  $p=0.029$ ;  $n=15$ , respectively). In all but three cases where ambient temperature information was available, die-offs were associated with



Table 2. List of colonies affected in the Northern Rivers region (NSW, Australia) during the temperature extreme of 12 January 2002.

colony <sup>a</sup>	15.00 hours air-temperature at nearest weather station (°C)	estimated number of <i>P. poliocephalus</i> and <i>P. alecto</i> present	% <i>P. alecto</i> among <i>Pteropus</i> spp. present	estimated minimum number of <i>Pteropus</i> spp. that died	% <i>P. alecto</i> among <i>Pteropus</i> spp. that died
Lumley Park	41.7	4000	35.0	51	98.0
Booyong	41.8	15 000	33.3	200	97.8
Dallis Park	42.9	28 000	42.9	1453	91.9
Coffs Creek	43.3	3600	—	75	6.7
Moore Park <sup>a</sup>	42.9	—	—	500	85.0
Kyogle 2002 <sup>a</sup>	43.2	—	—	300	100.0
Casino	43.3	—	—	affected	—
Currie Park <sup>a</sup>	42.4	24 000	50.0	1000	87.9
Mollies Grass	42.4	2000	50.0	100	80.0

<sup>a</sup> These colonies were also occupied by the unaffected *Pteropus scapulatus*, a smaller congener with a more inland distribution (Hall & Richards 2000).

temperatures that exceeded 42°C. We recommend active monitoring of colonies that are in areas where temperatures exceeding 42°C are predicted and encourage the reporting of any die-offs to us and the FFICN.

All die-offs occurred during the austral summer months. Unfortunately, owing to the difficulties of measuring rapidly decomposing bodies and catching live *Pteropus* individuals, it was not possible to compare biometrics of the individuals that died with those that survived. However, body condition of *P. poliocephalus* and *P. alecto* reaches its peak during summer (Welbergen 2005; D. Pinson 2002, personal communication), and therefore it is unlikely that body condition plays an important causal role in the die-offs.

Where mixed-species colonies were affected (i.e. Northern Rivers area, 2002; Ipswich, 1994 and 1999; table 3), *P. alecto* suffered substantially higher mortality than *P. poliocephalus* (this paper; N. Markus & L. Hall 2000, unpublished data), again suggesting that *P. alecto* is more sensitive to high temperatures than *P. poliocephalus*. *Pteropus alecto*'s Australian distribution is in tropical coastal regions (figure 2) where temperature extremes are less severe than within the more temperate coastal range of *P. poliocephalus* (e.g. Dury 1972; see also figure 2 in the electronic supplementary material). No deaths have been reported among *Pteropus scapulatus*, a smaller species of Australia's hot and arid interior (Hall & Richards 2000), even though on 12 January 2002 it was present in some affected colonies (table 2). *Pteropus scapulatus* is much less sensitive to hyperthermia than *P. poliocephalus* and temperatures in its range frequently exceed 42°C (ABM; Bartholomew *et al.* 1964; Dury 1972).

Half of the reported die-offs occurred south of the current southern distribution limit of *P. alecto* (figure 2), and an estimated minimum of 24 500 *P. poliocephalus* died during these events alone (table 3). *Pteropus poliocephalus*, once considered an abundant species with numbers estimated in the many millions (Ratcliffe 1931), has a current population size of less than 400 000 individuals, with a 30% decline between 1989 and 2001 (Eby & Lunney 2002). There is a general agreement that climate change will lead to an increase in the frequency, intensity and duration of temperature extremes (Meehl & Tebaldi 2004), and this is likely to pose a significant additional

threat to the survival of this vulnerable species and the important ecosystem services it provides.

We found only anecdotal evidence for three die-offs that occurred before 1994 (table 3). This suggests that die-offs have recently become more common; however, we cannot exclude the possibility that recent events are more likely to have been reported, owing to factors including increased environmental awareness and recent encroaches of human development on flying-fox habitat. Nevertheless, a recent increase in the number of die-offs is to be expected given that during the last 50 years occurrences of extreme heat events have increased in Australia (Hughes 2003). In particular, the average temperature has risen by approximately 0.17°C per decade in the area where die-offs have occurred (see Jones *et al.* 1999, using grid boxes –20° S to –40° S and 145° E to 155° E), and it is probable that this was accompanied by an increase in the frequency and duration of local temperature extremes (Easterling *et al.* 2000a; Schär *et al.* 2004).

*Pteropus alecto* has expanded its breeding range in eastern Australia by more than 750 km southwards in the past 75 years (Ratcliffe 1932; Nelson 1965; Eby & Palmer 1991); this southern expansion has coincided with a northern contraction of the range of *P. poliocephalus* by 250 km (Eby 2000). Temperature extremes increase in severity with latitude in eastern Australia (ABM; Dury 1972); therefore, the southern expansion of *P. alecto*'s range boundary puts the species at increased risk (see also figure 2 in the electronic supplementary material). Indeed, all but two of the reported die-off events occurred south of *P. alecto*'s 1928 southern distribution limit. It is unlikely that *P. alecto* will adapt quickly to the changing temperature regime because the species is considered essentially panmictic (Webb & Tidemann 1996) counteracting local adaptation at the expanding range boundary (Lenormand 2002). Interestingly, it has been suggested that increases in rainfall and average temperature in eastern Australia may have favoured the southern expansion *P. alecto* due to a reduction in the number of nights with frost, which the species cannot tolerate (Tidemann 1999). If so, this provides an example of how climate change may act like a double-edged sword: it can cause a species to expand its distribution in response to a reduction in the number of cold nights, while putting the same species at an increased risk from extreme warm events.

Table 3. List of past mass die-off events in eastern Australia.

no. <sup>a</sup>	date	area	state	maximum temperature at the nearest weather station	minimum number of colonies affected	estimated number of <i>Pteropus</i> that died		species present in affected area <sup>b</sup>	source
						min	max		
1	Feb 1791	Sydney	NSW	—	—	—	—	P	Tench (1793)
2	Dec 1905	Heildon	NSW	—	—	—	—	P	Ratcliffe (1932)
3	Jan 1913	Mallangance	NSW	—	—	—	—	P	Ratcliffe (1932)
4	Jan 1994	Townsville	QLD	44.3	1	—	—	A	J. Luly; FFICN
5	Jan 1994	Ipswich	QLD	44.3	1	1000	1000	A/P	own data
6	Dec 1994	Cabramatta; Gordon	NSW	43.2–43.9	2	6000	6000	P	M. Beck; Ku-ring-gai Bat Conservation Society
7	Jan 2000	Ipswich	QLD	40.7	1	500	500	A/P	own data
8	12 Jan 2002	Northern Rivers (see table 2)	NSW	41.7–43.3	9	3500	3500	A/P	own data
9	18 Jan 2003	Cabramatta	NSW	44.5	1	3500	3500	P	M. Beck; Ku-ring-gai Bat Conservation Society
10	3 Jan 2003	Gordon	NSW	44.0	1	1500	1500	P	M. Beck; Ku-ring-gai Bat Conservation Society
11	7 Jan 2004	Bellingen	NSW	43.7	1	3000	8000	P	M. Smith; NSW National Parks and Wildlife Service
12	1 Dec 2004	Coff's Harbour	NSW	41.1–44.8	2	1000	5000	P	J. Wood; FFICN
13	18 Dec 2005	Townsville	QLD	41.0	1	500	500	A	J. Luly; FFICN
14	24 Dec 2005	Wingham	NSW	43.3	1	5000	8000	P	L. Pope; FFICN
15	31 Dec 2005	Melbourne	VIC	42.9	1	113	400	P	L. Pope & Megan Davidson; FFICN
16	1 Jan 2006	Sydney, Central Coast	NSW	44.4–45.2	5	4230	4800	P	G. Parry-Jones; FFICN
17	22 Jan 2006	Melbourne	VIC	42.4	1	43	43	P	L. Pope; FFICN
18	10 Dec 2006	Melbourne	VIC	42.5	1	198	198	P	L. Pope; FFICN
19	16 Jan 2007	Melbourne	VIC	41.5	1	9	9	P	L. Pope; FFICN

<sup>a</sup> For locations of die-offs and distributions of affected species, see figure 2.<sup>b</sup> P, *P. poliocephalus*; A, *P. alecto*.

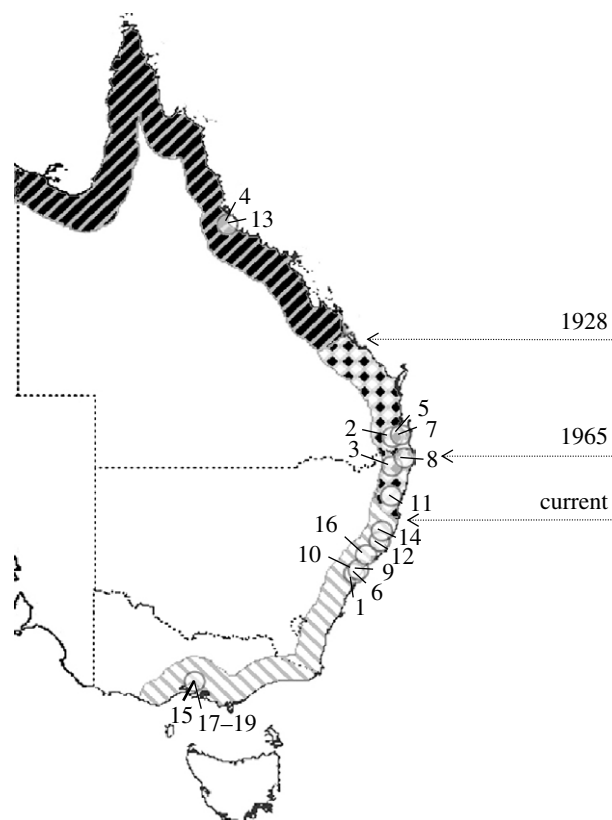


Figure 2. Distributions of *P. alecto* (right hatches) and *P. poliocephalus* (left hatches) and their current zone of overlap (checked) in eastern Australia. Dashed arrows show the southern latitudinal extent of *P. alecto* in 1928, 1965 and 2007. Bold numbers 1–19 represent general locations of past die-off events (details in table 3).

Climate change is likely to have profound impacts on the natural environment (Thomas *et al.* 2004); however, little is known about the kinds of effects of temperature extremes on natural systems. The divergent susceptibilities of *P. alecto* and *P. poliocephalus* to temperature extremes indicate that temperature extremes could mitigate the increased competition between the species that has been cited as another reason for the current demise of *P. poliocephalus* (Eby *et al.* 1999). This provides an example of how climate change may affect the connectedness in current ecosystems by influencing the dynamics between closely interacting or competing species. These kinds of complex dynamics are likely to complicate further predictions of ecological responses to climate change (e.g. Walther *et al.* 2002; Root *et al.* 2003).

The higher susceptibilities of adult females and dependent young indicate that temperature extremes can have disproportionate effects on effective breeding population and recruitment, two key parameters for conservation. Although the relative role of extreme temperature events as compared with climate means in affecting species' characteristics such as demography and distribution is still largely unknown (Easterling *et al.* 2000b), in species such as flying-foxes that have a very low natural capacity for increase (McIlwee & Martin 2002), factors that undermine recruitment and the effective breeding population are expected to exacerbate the threat to species survival in addition to the anthropogenic factors that have already been identified.

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